Multiple Modes of Asexual Reproduction by Tropical and Subtropical Sea Star Larvae: an Unusual Adaptation for Genet Dispersal and Survival

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Abstract. Sea star larvae (Echinodermata: Asteroidea), collected from the subtropical Northwest Atlantic Ocean, exhibited three distinct modes of asexual reproduction. A number of different bipinnariae and brachiolariae reproduced by paratomous cloning of the posterolateral arms. This morphogenesis was identical to that of larvae assignable to the genus *Luidia*. A second mode of asexual reproduction involves the autotomization of an anterior portion of the preoral lobe. Primary larvae with preoral lobes of varying sizes and free-swimming preoral lobes of various stages of morphological development were simultaneously collected. The free-swimming preoral lobes developed complete digestive systems and ultimately assumed the form of typical bipinnaria larvae. Asexual reproduction by larvae may also take the form of budding. The released individual is either a blastula- or gastrula-stage embryo. Subsequent development to a bipinnaria-stage secondary larva, with the possible exception of coelom formation, appears to occur through the events associated with normal larval development. These diverse methods of asexual propagation provide a common mechanism to increase the length of larval life and amplify the number of individuals. Thus asexual reproduction by larvae should increase the likelihood of genet representation in the next generation.

Introduction

The primary ecological role of planktonic invertebrate larvae is to disperse away from parent populations and recruit into habitats suitable for postlarval growth, development, and survival. Dispersal and successful recruitment of planktonic larvae regulates, in part, the geographical distribution of many benthic marine invertebrates (Thorson, 1950; Mileikovsky, 1971; Strathmann, 1974; Jackson and Strathmann, 1981; Roughgarden *et al.*, 1988). The arrival of competent larvae at suitable habitats is influenced by both abiotic and biotic features of the overlying water column (Pechenik, 1987; Strathmann, 1987; Young and Chia, 1987). Potential recruits can be lost to predation (Rumrill, 1990), starvation, and food limitation (Olson and Olson, 1989, and references within), and to dispersal away from appropriate settlement sites (Crisp, 1974; Jackson and Strathmann, 1981; Palmer and Strathmann, 1981; Roughgarden *et al.*, 1988). The greater the time that is required to complete the larval life, the more likely, in theory, that a given larva will be lost from recruitment.

Despite the theoretical disadvantages of a lengthy planktonic existence, larvae of many marine invertebrates are long-lived and potentially able to disperse over large geographic distances (*e.g.*, Thorson, 1961; Scheltema, 1964, 1966, 1971a, b; Scheltema and Williams, 1983). For example, planktotrophic larvae of many phyla (*e.g.*, Mollusca, Sipuncula, Echinodermata, and Brachiopoda) have been collected from surface plankton tows in all major currents of the North Atlantic gyre (Scheltema, 1964, 1966, 1971a, b, 1975; Laursen, 1981; Rice, 1981). Scheltema (1971a) labeled these larvae *teleplanic* ("far wandering") in reference to their potential for long-distance dispersal. Presumably, teleplanic larvae possess morphological, behavioral, and chemical characters and character states that decrease the likelihood of mortality during a

long dispersal phase. These larvae often possess expansive locomotory and feeding appendages, long elaborations of the body, and poorly calcified structural elements (*i.e.*, shell) (Scheltema, 1971a, b; Wilson, 1978; Domanski, 1984). These features are thought to decrease the rate of sinking and increase the volume of water cleared during feeding. In addition to structural alterations, changes in the physiological state of the larvae may also allow for an extended planktonic existence. Teleplanic larvae are thought to enter a metabolic steady-state (*i.e.*, growth stasis), where the energy demands of metabolism covary with the amount of ingested foods (Scheltema, 1966; Pechenik *et al.*, 1984). If the total energy cost of larval development is fixed for a species (Hoegh-Guldberg and Manahan, 1991), then the flexibility to vary development and metabolic rates with nutrient availability may be a prerequisite for a long larval life.

Yet adaptations that increase the likelihood that the genet (*i.e.*, a genetically discrete individual) will persist can take a different and novel form. Bosch (1988) and Bosch *et al.* (1989) reported that oceanic bipinnaria larvae of *Luidia* sp. (Ph. Asteroidea: Or. Paxillosida) reproduced asexually by paratomous cloning of the posterolateral larval arms. Upon release, the secondary embryos morphologically resemble late-stage gastrulae and rapidly assume the form of young bipinnaria larvae. Bosch *et al.* (1989) recognized that the ability of a larva to replicate itself may serve to lengthen the lifespan and size of each genet. These consequences of asexual reproduction by larvae may enhance the likelihood of successful recruitment into benthic habitats by (1) increasing the duration of the larval life (facilitating long-distance dispersal) and multiplying the number of larvae that may survive to metamorphic competence.

Further sampling has revealed that asexual reproduction by oceanic asteroid larvae in the tropical and subtropical Western Atlantic Ocean is restricted neither to a member of the genus *Luidia* nor to modifications of the posterolateral larval arms. Plankton samples taken in the Florida Current of the Gulf Stream and from the territorial waters of the Commonwealth of the Bahamas contained a number of different bipinnaria (with and without developing juveniles) and brachiolaria larvae that were reproducing asexually by one of three distinct modes. The potential for asexual reproduction has now been found in representatives of at least two different asteroid orders (Bosch, 1988; Bosch *et al.*, 1989; present study) and represents an unusual developmental adaptation to further the existence and lifetime of the genet.

Materials and Methods

Larvae were collected from surface waters (≤60 m in depth) of the Florida Current of the Gulf Stream (*ca.* 27.3°

N and 79.6° W to *ca.* 27.3° N and 78.8° W) and at various locations in the territorial waters of the Commonwealth of the Bahamas, chiefly in the area between the Berry Islands (*ca.* 25.5° N, 77.5° W), Eleuthera Island (*ca.* 25.5° N, 76.8° W), and Andros Island (*ca.* 25° N, 77.5° W) and off Grand Bahama Island (*ca.* 26.5° N; 78.8° W). All plankton samples were taken using a 3/4-m diameter net with a 202-μm (pore size) netting that was towed either horizontally or vertically. Sea star larvae were sorted from the total catch as soon as possible after collection and placed in seawater that had been filtered through a bag or string filter (*ca.* 5-μm pore size). Larvae that were maintained in the laboratory were held in finger bowls at 21–25°C and fed a mixture of *Dunaliella tertiolecta* and *Isochrysis galbana* (Tahitian strain). Each day the dishes were inspected for newly released secondary larvae and embryos. All asexually produced individuals were pooled and maintained in the same manner as the primary larvae. With the sole exception of the larva of a species assignable to the genus *Luidia* (Bosch *et al.*, 1989, see below), the taxonomic classification of the examined larvae remains unknown.

Bipinnaria larvae, brachiolaria larvae, and asexually produced individuals were processed in two ways for morphological inspection. For examination of larval gross anatomy, larvae were examined live or fixed in Hollande's fluid (Galigher and Kozloff, 1971) for 24 h, dehydrated with an ascending ethanol series, and examined using both a compound and a dissecting microscope. For studies of external and internal surfaces, larvae and embryos were fixed in 1% OsO_4 in either seawater or distilled water for 1 h, serially dehydrated with ethanol, and critical-point-dried using CO_2 as the transition fluid. The specimens were mounted on stubs, coated with a gold-palladium mixture, and then examined using a Novascan 30 scanning electron microscope.

Results

Field-collected bipinnaria and brachiolaria larvae exhibited three forms of asexual reproduction. Asexually produced individuals were either (1) released as late gastrula-stage embryos or early bipinnaria larvae from either or both posterolateral arms of primary larvae (Figs. 1, 4, 6), (2) developed from an autotomized anterior region of the preoral lobe (Figs. 8–9), or (3) released from the apical tips of the arms of primary larvae in a blastula- or gastrula-like condition (Figs. 2, 3, 14, 15). Based on the morphology and coloration patterns of the examined larvae, it is assumed that each of the three modes of asexual reproduction is exhibited by different species.

The most common method of asexual reproduction observed was the differentiation of either a single or both posterolateral arms to become modified into secondary
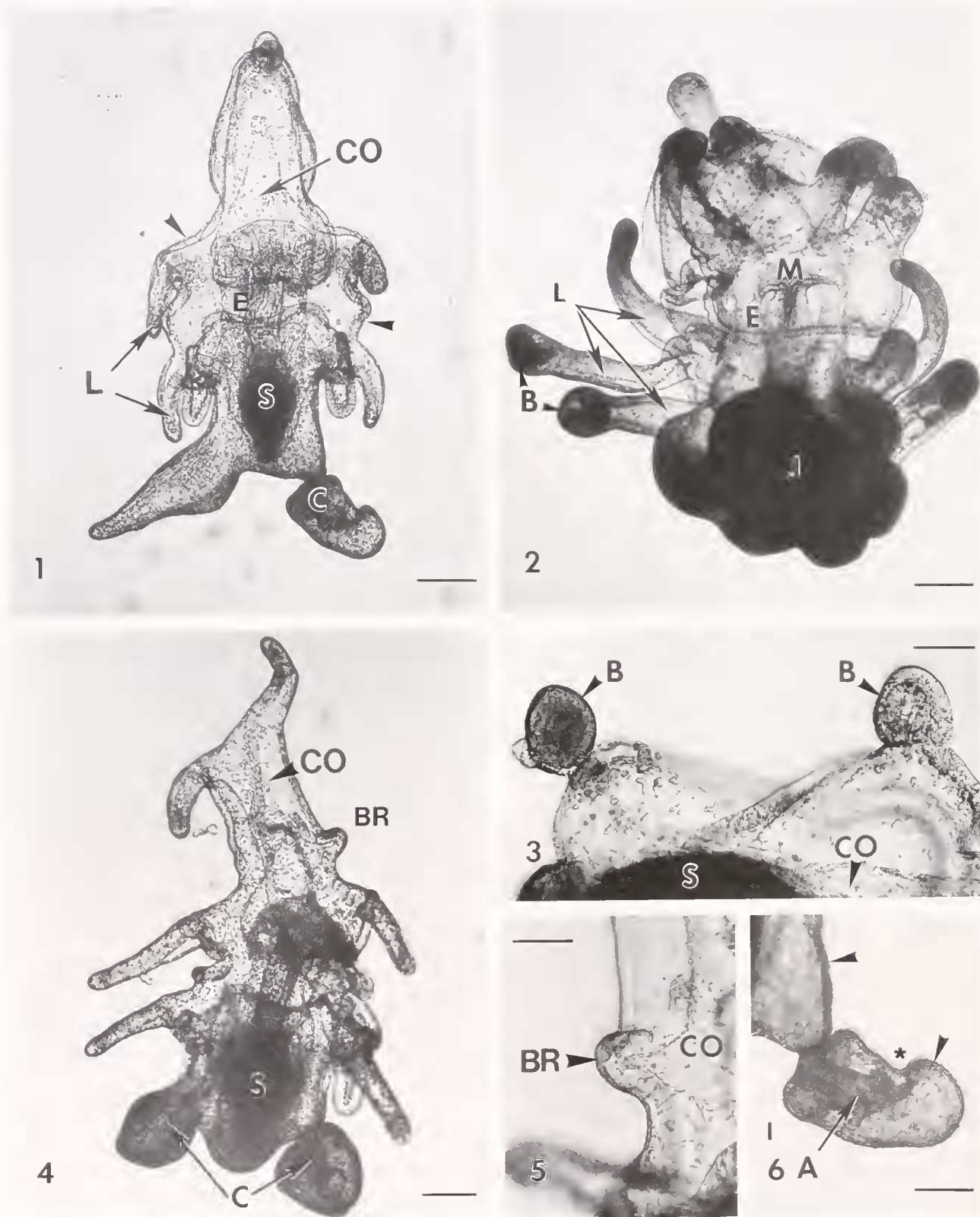
Figures 1-6. Light micrographs of asexual reproduction via paratomous cloning and budding by field-collected bipinnaria and brachiolaria larvae.

larvae (Figs. 1, 4). This mode of asexual propagation was originally described by Bosch *et al.* (1989) for larvae assignable to the genus *Luidia.* In addition to bipinnariae of *Luidia* sp., a number of field-collected brachiolaria larvae also underwent asexual reproduction by modification of the posterolateral larval arms (Fig. 4; note that members of the order Paxillosida do not develop a brachiolaria-stage larva). Although the brachiolar complex was not well formed in any asexually reproducing larva, each possessed a pair of arms on the ventral face of the preoral lobe that contained an extension of the anterior larval coelom; hence these are here considered to be brachiolar arms (Fig. 5). Secondary larvae from both bipinnariae and brachiolariae are generally released as late gastrulae or early bipinnariae. Many attached secondary larvae developed a ciliary band, and the primordium of the circumoral field is evident (Fig. 6). In some exceptional individuals, primary larvae were collected with fully formed secondary bipinnaria larvae still attached.

Asexual reproduction exhibited by oceanic asteroid larvae may also involve the apparent autotomization of the anterior portion of the preoral lobe. A number of morphologically identical bipinnaria larvae of similar body size (here defined as the distance between the posterior margin of the larval body and the posterior margin of the preoral lobe) were obtained from a single plankton tow taken in the Florida Current of the Gulf Stream. Although the body size was similar among individuals, the size of the preoral lobe ranged from complete (Fig. 7) to absent (Fig. 10), with individuals intermediate between the two extremes also present (Fig. 11). The loss of the anteriormost portion of the larval body is probably not an artifact of the collection method because intermediate forms are present (Fig. 11) and close examination of the site of autotomization does not reveal any evidence of mechanically induced tissue damage (Fig. 12). Collected alongside larvae exhibiting preoral lobes of various sizes were a number of free-swimming preoral lobes that developed a complete digestive system (apparently from larval ectoderm) 1–2 days after collection (Figs. 8, 9). The newly released individuals retain a portion of the coelomic system of the primary larva from which the remainder of the secondary larva's coelomic system is presumed to be derived (the assumed site of autotomization is depicted in Fig. 7). Secondary larvae retain the normal anterior-posterior polarity of the primary larvae. Although secondary larvae are initially asymmetrical about the anterior-posterior axis (with the preoral lobe being disproportionately large; Fig. 8), their posterior region presumably grows at an accelerated rate and these larvae assume the proportions of typical bipinnariae (Fig. 9).

A third method of asexual reproduction was infrequently observed and involved the release and subsequent development of a small apical portion of a larval arm. The initiation of larval budding (Figs. 2, 3) coincides with an accumulation of mesenchyme-like cells in the distal tip of the arm (Figs. 3, 13). The tip of each budding arm becomes swollen and rounded (Figs. 4, 13). The tissue linking primary larvae to their secondary embryos (Figs. 3, 14) regresses and the connection is lost. The newly released secondary individual is in a developmental state that is morphologically similar to either a blastula-stage (Fig. 15) or an early gastrula-stage embryo (Fig. 16). The apical surface of these cells is lined with microvilli, and each cell possesses a cilium (not shown). Secondary embryos have a blastocoelic space of variable size (Figs. 14–

Figure 1. Light micrograph of a bipinnaria larva of *Luidia* sp. (ventral view) reproducing asexually through paratomous cloning of the posterolateral arms. Note the difference in appearance between the posterolateral arms and other larval arms (L). The secondary larva (C) of the larval left side is near the point of release from the primary larva. The anterior extension of the anterior coelom (CO) has extended well into the preoral lobe. E—esophagus; S—stomach; arrowhead—ciliary band; scale bar = 65 μm.
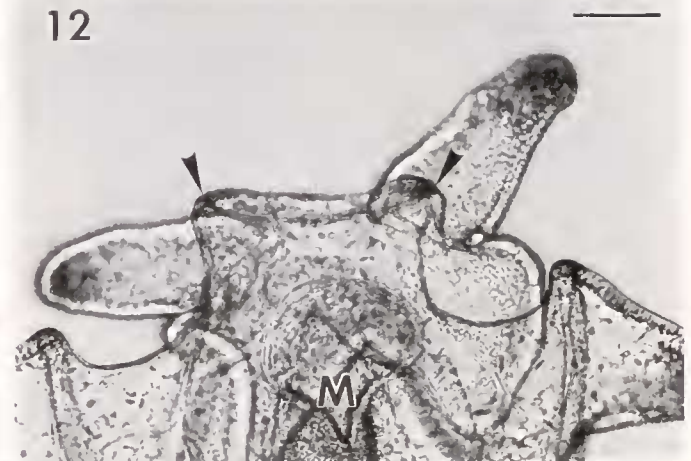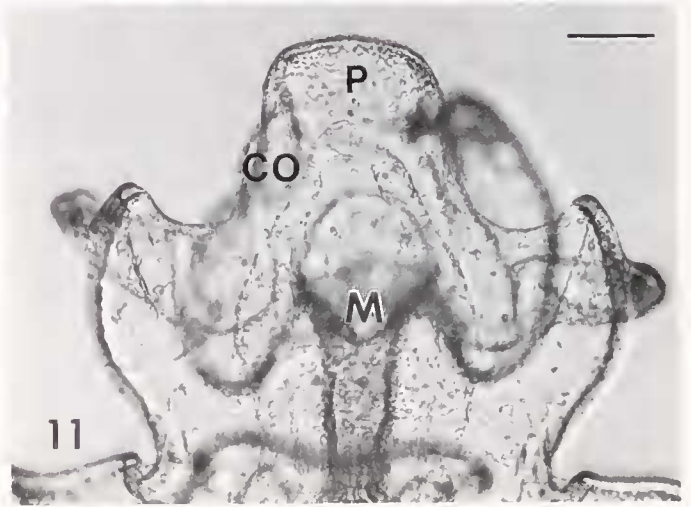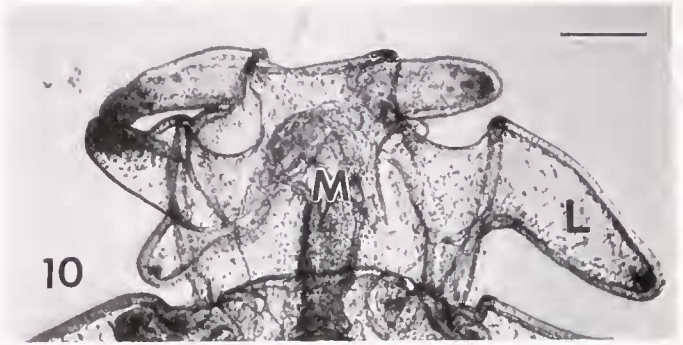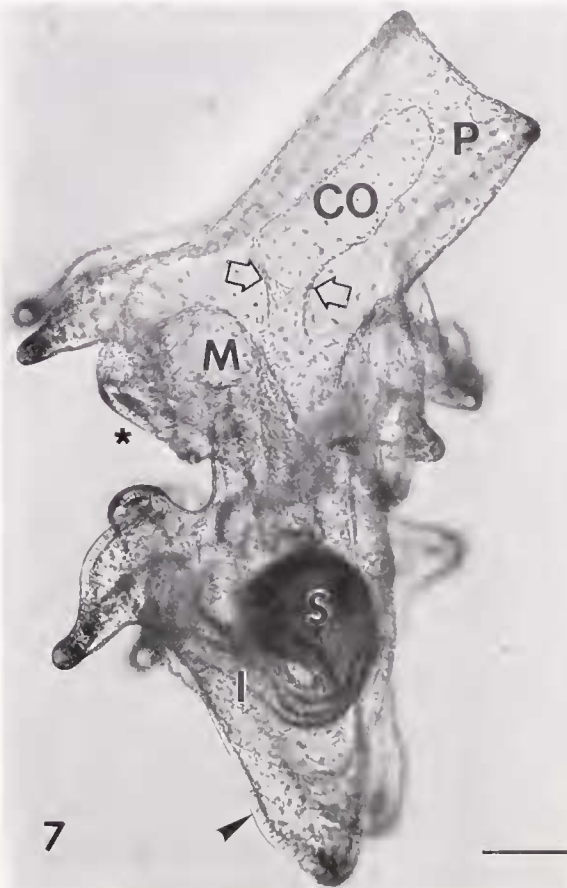
Figure 2. Light micrograph of a bipinnaria larva (ventral view) in the early stages of asexual reproduction via budding. Those larval arms that appear to be developing buds (B) differ in appearance from nonbudding larval arms (L). E—esophagus; J—developing juvenile; M—mouth; scale bar = 316 μm.

Figure 3. Light micrograph of the right ventral side of a larva reproducing asexually by developing buds (B). CO—right somatocoel; S—stomach; scale bar = 48 μm.

Figure 4. Light micrograph of a brachiolaria larva reproducing asexually via paratomous cloning of both posterolateral arms. The developing secondary larvae (C) differ in appearance from other unmodified larval arms. Examination of the preoral lobe reveals an extension of the anterior coelom (CO) into an evagination of the epithelium, producing a brachiolar arm (BR). S—stomach; arrowhead—ciliary band; scale bar = 65 μm.

Figure 5. Light micrograph of the brachiolar arm depicted in Figure 4 clearly showing the extension of the anterior coelom (CO) into the brachiolar arm (BR). Scale bar = 29 μm.

Figure 6. Light micrograph of a secondary individual produced by paratomous cloning of the posterolateral arms. The developing archenteron (A) and the beginning of the oral vestibule (*) are visible in this specimen. Arrowheads—ciliary band of both the primary and the secondary larva; scale bar = 39 μm.

Figures 7–12. Light micrographs of primary and secondary larvae that are involved in or the result of autotomization of the preoral lobe of bipinnaria larvae.

Figure 7. Light micrograph of a left lateral view of a fully formed bipinnaria larva showing the vestibule (*), mouth (M), stomach (S), and intestine (I). Within the preoral lobe (P), the anterior extension of the coelom (CO) is clearly evident. The assumed plane of autotomization is the area suggested by the space between the open arrows. Arrowheads—ciliated band; scale bar = 88 μm.

Figure 8. Light micrograph of a left side view of a developing secondary larva released through the autotomization of a preoral lobe. The digestive system is nearly fully formed. I—intestine; S—stomach; mouth vestibule—(*); scale bar = 70 μm.

Figure 9. A light micrograph of a right side view of a secondary larva that is more developed than the individual depicted in Figure 8. The ciliated band (arrowhead) is clearly differentiated from the other cells of the larval epithelium. I—intestine; S—stomach; scale bar = 100 μm.

Figure 10. Light micrograph showing a ventral view of a bipinnaria larva that has autotomized its preoral lobe. L—larval arm; M—mouth; scale bar = 158 μm.

16, 20) and within the blastocoel there can be a variable number of mesenchyme-like cells (Figs. 14–16, 20–21). If the secondary embryo is released in a blastula-like condition, the cells of one side of the secondary embryo begin to invaginate into the blastocoelic cavity (Fig. 16), ultimately resulting in the formation of a gastrula-like secondary embryo (Fig. 17). Development of the mesoderm of the secondary larva has not been directly observed. Thus coelomic development could occur either from outpocketings of the developing archenteron or from the pool of mesenchyme-like cells that preexist within the blastocoel and accumulate at the distal tip of the archenteron (Figs. 15–18, 20–21). As development proceeds, the cells of the outer epithelium become thinner in profile and the embryo elongates (Figs. 16–18). The developing archenteron comes in contact with the outer epithelium and a secondary opening, the mouth, is formed. The entire process (from release to a feeding individual) requires 24–36 h. In addition to elongation, the developing individual develops the ciliated bands and overall morphology of a bipinnaria larva (Figs. 18, 19).

Discussion

A majority of marine invertebrates produce planktonic larvae that remain in the water column for variable periods of time. This obligate dispersal period allows for (1) recruitment into sympatric populations, (2) maintenance of genetic communication between allopatric populations, and (3) colonization of new or recently opened habitats (e.g., Thorson, 1946, 1950; Scheltema, 1971a, b; Mileikovsky, 1971; Crisp, 1974, 1976; Chia, 1974). Dispersal increases the probability that a species will persist in both ecological and geologic time scales (Jablonski and Lutz, 1983). However, these positive benefits of a planktonic larval stage are countered by the increased likelihood of larval mortality with extended time in the plankton (Vance, 1973, 1974; Strathmann, 1974, 1985; Jackson and Strathmann, 1981; Young and Chia, 1987; Roughgarden et al., 1988). Much recent work on the ecology of invertebrate larvae has been centered on coastal larval forms (e.g., see Young, 1990). Dispersal away from neritic waters by local circulation patterns significantly decreases the likelihood of successful recruitment for coastal larval forms (Roughgarden et al., 1988). In contrast, teleplanic larvae, which possess structural, physiological, and reproductive characteristics to prolong larval life, can disperse great distances and recruit into habitats far from the source population (Scheltema, 1971a, b).

Discussions of the ecology of teleplanic larvae largely center on the velocity of the prevailing ocean currents and the adaptations (e.g., increased size of the feeding structures, decreased weight of inorganic structural elements, and growth stasis) that increase the probability of survival (e.g., Scheltema, 1966; Pechenik et al., 1984). Thorson (1961) believed that "long-distance larvae seem only to occur in special groups of prosobranchs and crustaceans" and doubted that echinoderm larvae were capable of transoceanic dispersal. Thorson did, however, note the observations of Mortensen (1921; p. 147–149) on an ophiopluteus larva (Ophiopluteus opulentus) that apparently released a benthic juvenile and then returned to the water column. This larva subsequently regenerated both the ciliary bands and the posterior digestive system and ultimately assumed the morphology of a normal larva. Thorson suggests that "some tropical ophiurans and perhaps some tropical asteroids may have chances to cross even the widest ocean basins, provided that Mortensen's observations on the 'budding larval polyps' holds true." The results of previous studies (Bosch, 1988; Bosch et al., 1989) and the present study reveal that asexual reproduction by echinoderm larvae exists and is not restricted solely to the ophiurans.

All modes of asexual reproduction described in this report involve a serial dedifferentiation and redifferentiation of larval tissue. In all three modes the primary developmental cycle (egg → embryo → larva) is overlapped by a new developmental series (primary larval tissue → secondary embryonic tissue → secondary larval tissue). In secondary larvae produced by all observed modes of asexual reproduction, it appears that the "endodermal" regions are derived from the primary larva's differentiated ectoderm. Further, the concordance between the position of the putative mesenchyme-like cells and the coelomic cavities in secondary larvae, produced either by paratomy or budding, suggests that these cells are responsible for or assist in the production of these mesodermal structures.

The process of asexual reproduction differs among the three modes described in this report. These developmental differences, coupled with the fact that larvae from at least

Figure 11. Light micrograph of a bipinnaria larva with a preoral lobe (P) of intermediate height (dorsal view, plane of focus is midfrontal). The connection between the left and right anterior coeloms (CO) is visible immediately anterior to the mouth (M). Scale bar = 62 μm.

Figure 12. Light micrograph of a higher magnification view of the larva shown in Figure 10. The smooth surface of the site of apparent autotomization is denoted by the arrowheads. M—mouth; scale bar = 91 μm.
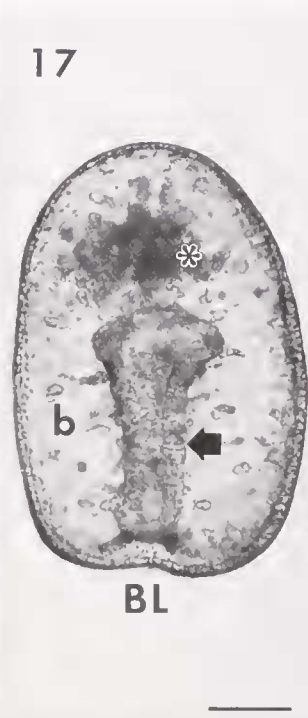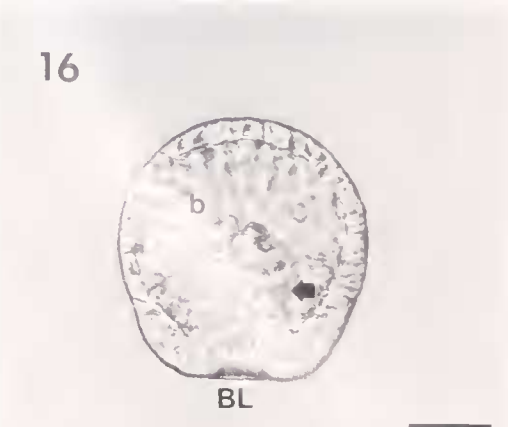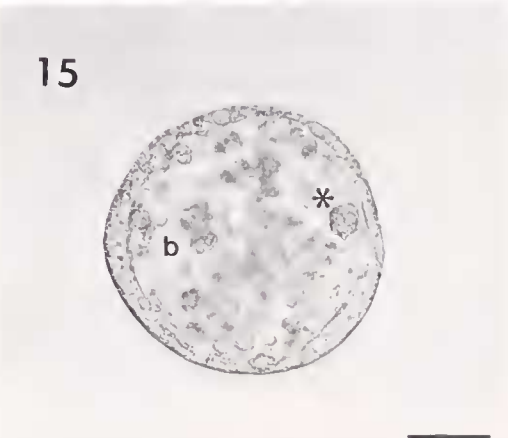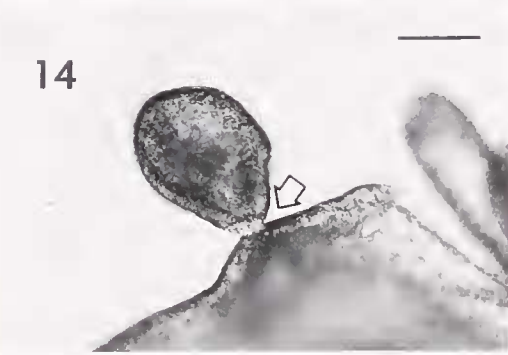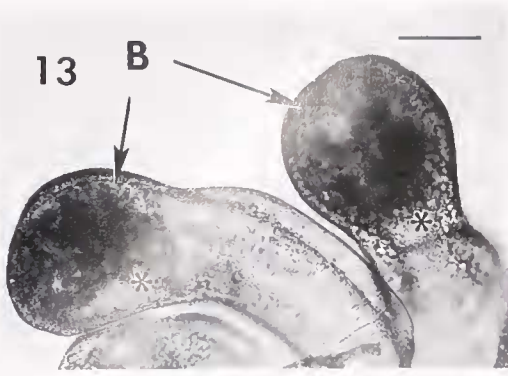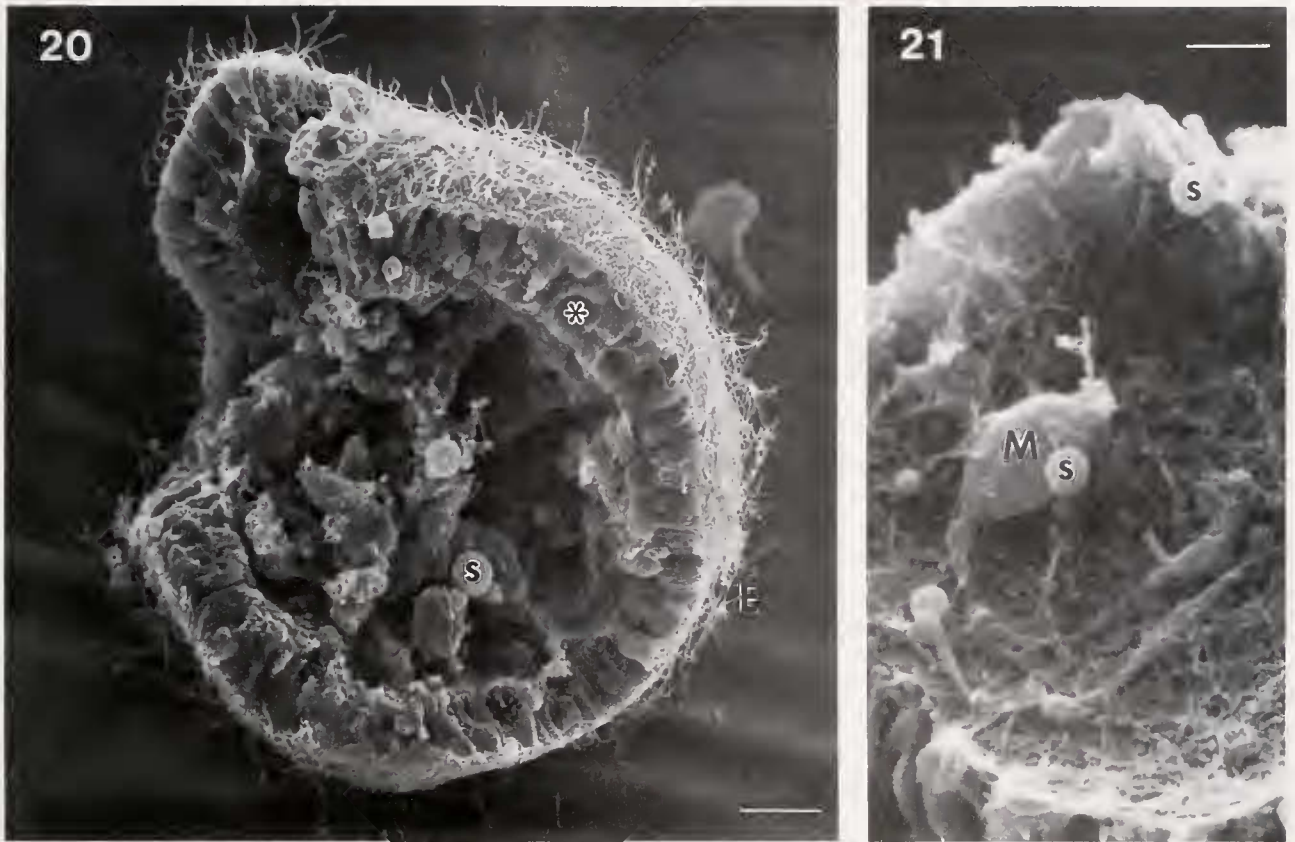
Figures 20-21. Scanning electron micrographs of the exterior and interior surfaces of newly released secondary embryos.

Figure 20. Scanning electron micrograph of a blastula-stage individual that has been broken open. The epithelium (E) is composed primarily of ciliated columnar cells, but circular holes suggest that at least one other cell type is present. The blastocoelic space is filled with cells; in this micrograph small spherical cells (S) are notable. Scale bar = 28 μm.

Figure 21. Scanning electron micrograph of the basal face of the outer epithelium of a blastula-stage embryo. Present are mesenchyme-like cells (M) and smaller spherical cells (S). The inner surface of the epithelium is lined with a fibrous meshwork. Scale bar = 9 μm.

Figures 13-19. Light and scanning electron micrographs that depict the sequence of events during the process of asexual reproduction by budding.

Figure 13. Light micrograph showing the rounded appearance of the arm apices (B) and the associated accumulation of cells (*). Scale bar = 58 μm.

Figure 14. Light micrograph of a bud near the time of release from the primary larva. The site of bud/larva junction is designated by the arrow. Scale bar = 38 μm.

Figure 15. Light micrograph of a released bud in a blastula-like condition. In this individual, the cell-free blastocoel (b) is small and the blastocoelic space contains a large number of cells (*). Scale bar = 33 μm.

Figure 16. Light micrograph of a free-swimming secondary embryo undergoing gastrulation. The developing archenteron (closed arrow) is formed by the invagination of the epithelium into the blastocoel (b). Blastopore—BL; scale bar = 25 μm.

Figure 17. A light micrograph showing a fully formed gastrula-stage secondary embryo produced by asexual reproduction by budding. The well-developed archenteron (filled arrow) leads from the blastopore (BL) into the blastocoel (b). The accumulation of cells at the apex of the archenteron (*) is seen in many individuals and may be involved in the formation of the coeloms of the secondary larva. Scale bar = 27 μm.

Figure 18. A light micrograph of a dorsal view of a newly formed secondary bipinnaria larva. The ciliated band (arrowhead) has formed and the primordium of the coelomic system of the secondary larva (CO) is clearly evident at the anterior extent of the developing larval gut (filled arrow). Scale bar = 23 μm.

Figure 19. Scanning electron micrograph of a fully formed secondary bipinnaria larva that developed from a bud released from a primary larva. Anus—A; mouth—M; ciliated band—(filled arrow); scale bar = 28 μm.

two orders are reproducing asexually (members of the order Paxillosida (*e.g., Luidia*) do not develop a brachiolar complex), suggest that asexual reproduction represents an adaptation to a prolonged planktonic existence. However, the factor or factors that regulate the production of secondary larvae remain obscure.

Despite the theoretical advantages of persistence and amplification of the genet, asexual reproduction may have a negative impact on the primary larvae. All forms of asexual reproduction require a relatively small percentage of the total larval soma, but may significantly reduce the effectiveness of larval feeding. In paratomous cloning (mode 1), each posterolateral arm is completely modified to produce a secondary larva. Although this arm pair is at the posterior margin of the larval body, it may contribute a significant percentage of the total number of food particles captured. Hart (1991) reported that the posterior region of the body of bipinnaria larvae of *Dermasterias imbricata* accounted for nearly a quarter of the observed particle captures. The small portion of an arm lost through budding (mode 3) is less likely to interfere with the particle capture mechanism to the same degree. In contrast, asexual reproduction by autotomization of the preoral lobe (mode 2) is predicted to have a significant impact on the feeding performance of the primary larva. Hart (1991) observed that 50% of the particle captures by larvae of *Dermasterias imbricata* were attributable to the ciliary bands anterior to the mouth.

The obvious benefit afforded a species by larval asexual reproduction is persistence of the genet through an increase in the number of propagules without a concomitant increase in the reproductive effort of the parent generation. The lengthening of the larval lifespan and the amplification of the number of larvae in the plankton should increase the probability of successful representation in the following generation. Persistence of three different modes of asexual reproduction, spanning at least two taxonomic orders, indicates that this adaptation to a prolonged planktonic existence is both ecologically and evolutionarily important.

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